

A CONTRIBUTION TO THE MORPHOLOGY OF *ZANNICHELLIA ASCHERSONIANA* GRAEBN.

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INTRODUCTION

When describing plants with extremely reduced floral parts and complex inflorescences, it is of the utmost importance that the gross morphology is fully understood.

In the case of the pondweed *Zannichellia aschersoniana* Graebn. (1907), the inadequate type description, which omitted the structure of the male flower altogether, has resulted in some confusion in subsequent accounts of the dispecific genus *Zannichellia* L. in general taxonomic works. For this reason, a detailed account of the morphology of *Z. aschersoniana* is given below.

The species, apparently endemic to the Cape South West, is an annual growing in seasonal vleis. Living flowering material from vleis just inshore from Table Bay near Paarden Island and Milnerton, near Kommetjie, on the Cape Flats, and near Hermanus and Lamberts Bay was examined, also type material: "Pools above Varsche Vlei" Wolley Dod, 3586 (BOL).

MORPHOLOGY

The size of the plant appears to be governed by the depth attained by the seasonal body of water in which it is growing.

Erect stems, with a diameter of about 0.6 mm. which may be branched and attain a length of up to 40 cm., arise at most nodes of a branched creeping rhizome. The leaf arrangement is alternate, and nodal lengths in erect stems of up to 6 cm. have been recorded. (Fig. 2A.)

Leaf length increases acropetally, but the degree of difference in length between leaves at basal and apical nodes varies from one to several centimetres. Mature leaf lengths of from 1.0 to 6.5 cm. have been recorded. The leaf blade has a central midrib, a rounded acuminate apex, and is 0.5 to 1.5 mm. wide. From the base of the leaf extending upwards for about 3 to 7 mm., depending

upon leaf length, the margins are expanded on either side to form a membranous sheath which completely encircles the stem at the node. This sheath forms a ligule-like projection at its apex, extending about 0.5 mm. above the line of fusion with the leaf (Fig. 2B). The membranous corners of this ligule are very slightly auriculate but often become eroded away during the life of the plant. In the very young stages this sheath forms a short tube around the stem, which later splits.

In the axil of each leaf, on either side of the axillary bud are two small membranous scales, usually about a millimetre in length and less than 0.1 mm. wide. The axillary buds are enclosed, whether vegetative or reproductive, by a membranous sheathing bract up to 6 mm. long.

The rhizome also bears leaves at the nodes similar in structure to, but generally shorter than, those on the erect stems; these usually fall away during the life of the plant. Also at each node, one to several adventitious roots arise, with a fine covering of root hairs for their entire length, which may be up to 20 cm. When the adventitious roots first appear they are enclosed in a protective sheath which persists as a small collar of tissue 0.1 mm. long at the base of the root. The diameter of the rhizome is the same as that of the erect stem, and that of the adventitious roots is about 0.3 mm. Rhizome nodal lengths of up to 2.5 cm. have been measured.

Where upright stems occur at the nodes, growth is sympodial; the main axis continues as the erect shoot, while the rhizome is continued by growth of an axillary branch. At the point where it arises in the axil of what must be now considered the basal leaf of the erect shoot, the rhizome is encircled by a membranous sheathing bract about 3 to 5 mm. long (see Fig. 2C). At first this bract is tubular but later it splits from the apex downwards and eventually may fall away. This bract and those surrounding the axillary buds of the erect shoots may be considered as modified first leaves of axillary shoots.

The inflorescences are axillary, male and female being borne together in a compound inflorescence of a sympodial nature (Fig. 1A, B). At the base of the inflorescence is the aforementioned membranous bract (Fig. 1A, B, a) which, in the early stages, forms a sheath-like cap completely enclosing the developing inflorescence (Fig. 1C). Later this sheath splits, and at floral maturity it is spathe-like, about 3 to 6 mm. long and 1.5 to 2 mm. wide.

The lower first inflorescence axis generally terminates in a male flower, and on this axis is borne a second modified foliage leaf (Fig. 1A, B, b). The shape and degree of development of this leaf varies considerably (Fig. 1D). When mature it may be entirely membranous with a central projection indicating an extremely reduced lamina, or the central projection may be more pronounced, with a green tip, or there may be a definite demarcation between a central green

lamina and a membranous sheathing base. No cases were found where the sheathing base had become ligulate. In length this leaf varies from about 2.5 to 4.5 mm., its width (at its widest part) is about 1 mm.

In the axil of this leaf is a second upper inflorescence axis which usually terminates in a female flower. This second axillary inflorescence is surrounded by a second membranous sheath (Fig. 1A, B, C) similar in structure and development to the membranous bract surrounding the first axis; at floral maturity this may be 2 to 4.5 mm. long and 1 to 1.5 mm. wide. Just below the terminal flower is another modified foliage leaf (Fig. 1A, B, D). Again the degree of development of this is variable, but it is generally more leaf-like than the equivalent leaf on the lower inflorescence axis, with a prominent central green lamina. In the axil of this leaf is an axillary bud, protected by the usual membranous sheath, which in most cases remains dormant. However, it may grow out to form a third inflorescence axis or a vegetative shoot. In this event, the subtending leaf may develop a ligulate base and attain a length of over a centimetre. On the other hand, when the axillary bud is poorly developed the subtending leaf may be very small and membranous.

The flower on the lowest axis matures first. While the first axis of this cymose inflorescence usually terminates in a male flower and the second in a female flower, other arrangements are not uncommon. The order may be reversed, or both flowers may be of one sex, or, rarely, only one flower may develop.

The male flower (Fig. 1E) consists of a single compound stamen borne on a long slender stalk, about 25 mm. long at the time of anther dehiscence, and 4 apical anther lobes, each about 3 to 4 mm. long and dehiscing by means of a longitudinal slit (the mature pollen is globose). There is a conical projection, about 1 mm. long or less, of the anther connective above the anthers. The bases of the anther lobes are free from the central stalk for about one quarter of their length, and in the early stages of development each lobe is bilocular. It is probable that these represent two fused bilobed anthers. The question arises whether the stalk upon which these are borne is a compound filament or a pedicel. At the base of this stalk, several small hair-like membranous scales about one mm. long are to be found, which are extremely difficult to dissect out. It was at first suspected that these might represent a perianth at the base of a compound filament, but it is more likely that they are morphologically similar to the two small scales found in the axils of every normal foliage leaf.

The female flower (Fig. 1F) has a short peduncle, 0.2 mm. long, above the reduced foliage leaf. There is a sac-like membranous perianth which surrounds the single carpel and part of the style. The ovary is unevenly inflated so that one side of it bulges more than the other. The style ranges from 1 to 2 mm. in length,

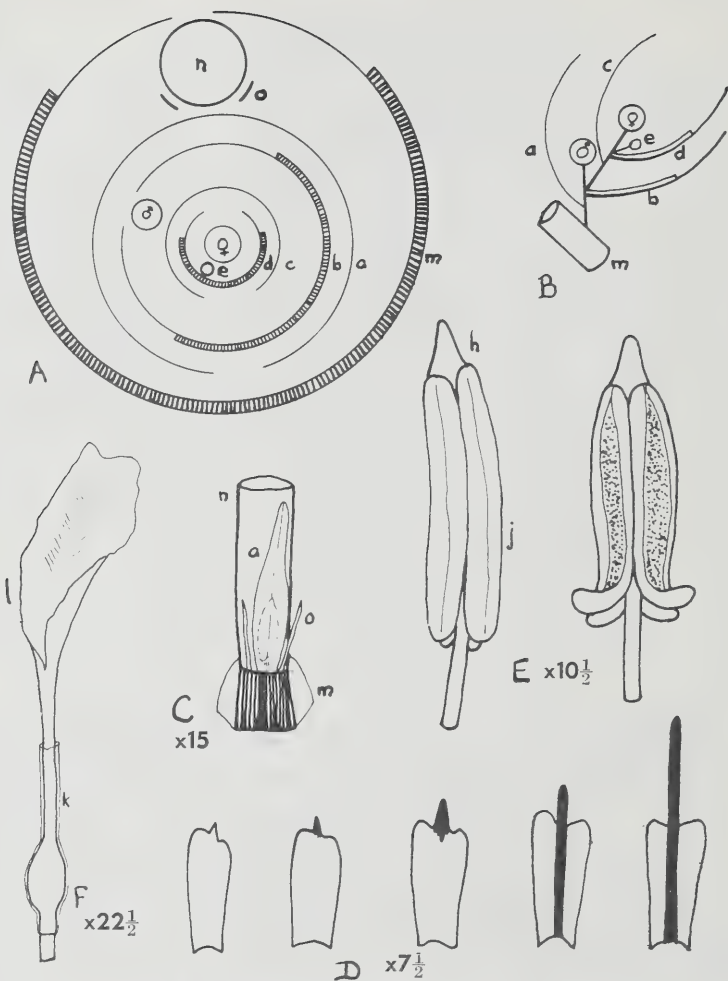


FIG. 1. A and B, diagrams of inflorescence (in B the length of inflorescence axes is greatly exaggerated): *m* leaf on main stem *n*, *o* scales on either side of axillary bud, *a* membranous bract at base of first axis, *b* reduced leaf on first axis subtending second axis, *c* bract at base of second axis, *d* reduced leaf on second axis subtending undeveloped axillary bud *e*; C leaf bent back showing young axillary bud enclosed in membranous sheath $\times 15$; D different degrees of development of leaf *b* $\times 7\frac{1}{2}$; E male flower before and after dehiscence $\times 10\frac{1}{2}$; *h* projection of anther connective, *j* one of 4 anther lobes; F young female flower $\times 22\frac{1}{2}$; *k* sac-like perianth, *l* funnel shaped stigma.

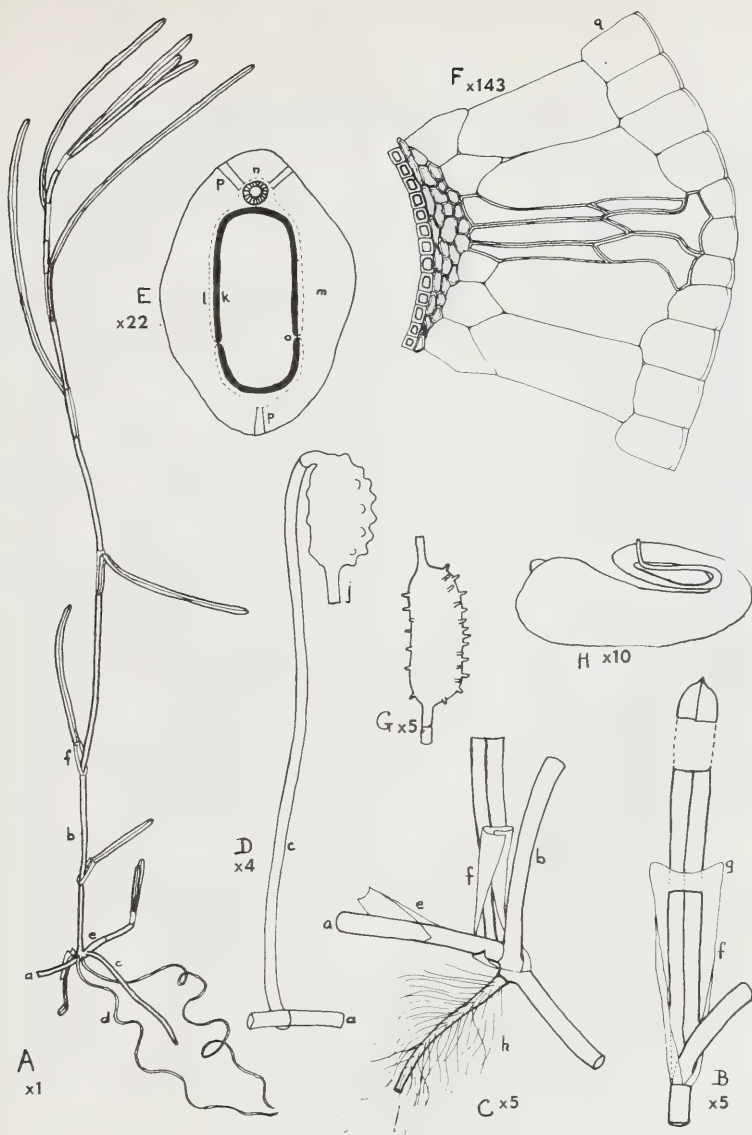


FIG. 2.—A portion of plant showing part of rhizome *a*, and an erect shoot, *b*, $\times 1$; *c* positively geotropic fruit peduncle, *d* adventitious root, *e* basal sheath of new rhizome axis, *f* sheathing leaf base; B leaf $\times 5$; *g* ligulate extension of sheathing base; C portion of rhizome showing sympodial growth $\times 5$; *h* root hairs; D green fruit from rhizome node $\times 4$; *j* remains of style; E diagram of transverse section of pericarp $\times 22$; *k* inner cuboidal cells, *l* small squashed cells, *m* outer parenchyma layers, *n* vascular strand surrounded by sclerenchyma sheath, *o* thin-walled cells of endocarp, *p* groups of slightly lignified elongated cells; F anatomical detail of pericarp wall $\times 143$; *q* epidermis; G old pericarp with outer layers sloughed off $\times 5$; H embryo with coiled cotyledon $\times 10$.

and terminates in a funnel-shaped stigma, elongated on one side (up to 2 mm. in some mature forms).

At maturity the fruits are stalked. Those fruits borne on inflorescences arising in the axils of rhizome leaves, and the lower leaves of erect shoots, are up to 4 cm. long and positively geotropic, burying the fruit in vlel mud. The peduncles of fruits borne higher up on erect shoots are only a few mm. in length—often not more than one millimetre. The slight uneven inflation of the ovary is more emphasised in the fruit. The style is persistent, the funnel-shaped stigma withers away.

While still green, the pericarp has a patterning of warty protuberances and when mature may be 3 to 4 mm. long and 1.0 to 2.5 mm. wide (Fig. 2D). In transverse section the fruit is oval (Fig. 2E). The innermost layers of the pericarp consist of small cuboidal cells whose walls are heavily lignified; to the outside of these is a unicellular layer of small, somewhat squashed cells with slightly thickened walls. At each end of the oval, that is in lines running down the dorsal and ventral sides of the pericarp, this layer is several cells thick. At one end of the oval a small vascular strand surrounded by a sclerenchyma sheath abuts onto this layer of squashed cells. Towards the opposite end, on either side, is a point where a few of the cuboidal endocarp cells, and the small squashed cells to the immediate outside of these, are thin walled. This results in two V-shaped grooves—presumably the future lines of dehiscence of the pericarp.

Between the small squashed cells and the outer epidermal cells, is thin-walled, spongy chlorophyll containing parenchyma, usually in two layers, the inner smaller, the outer larger. The outer walls of the epidermal cells have a slight cellulose thickening.

At intervals, usually not more than four being seen in any transverse section, groups of elongate slightly lignified cells extend from the small layer of squashed cells to the epidermis, resulting in the warty protuberances seen in the green pericarp (Fig. 2F). As the pericarp matures the inner cuboidal cells, the squashed small cells and the groups of lignified elongated cells become suberised. The epidermis and spongy parenchyma cells slough off, leaving the dark brown inner layers of the pericarp, with spiny projections up to 0.3 mm. long, near the dorsal and ventral edges of the laterally compressed fruit (Fig. 2G).

The seed is pendulous, the placenta being on the inflated side of the ovary wall, just below the base of the style. Removal of the membranous testa exposes the single coiled cotyledon (Fig. 2H).

On the Cape Peninsula and Cape Flats the seasonal vleis are normally completely dry by the end of November. On the surface of the sun-baked mud, old *Zannichellia* plants form a thin dry mat, in which are entangled dormant fruits. Those fruits which developed on the lower parts of the plant may have been pushed into the mud by their long positively geotropic pedicels. Presumably

this affords greater protection in cases of extreme drought. Germination starts soon after the first rains begin to fill the vleis.

TAXONOMIC NOTE

In Ascherson & Graebner's classification (1907) of the Potamogetonaceae, *Zannichellia* L is placed in the tribe Zannichellieae Kunth., distinguished by unisexual flowers, the persistent presence of a perianth in the female flower and weakly saline or fresh water habitat. This tribe is divided into two genera, *Zannichellia*, characterised by naked male flowers and female flowers with a cup-like perianth enclosing one to eight free, slightly curved carpels; and *Althenia* Fr. Petit, with a short cup-like perianth in the male flower and a perianth of three bracts surrounding three straight carpels in the female flower.

Althenia is divided into two sections, *Eualthenia* Graebn., consisting of one species *A. filiformis* Fr. Petit and *Lepilaena* (Drumm.) Aschers., now reinstated as a separate genus by most taxonomists. In *Lepilaena* Drumm. of Australia and New Zealand the androecium consists of two or three fused bilobed anthers immediately below which is a short, cup-shaped perianth, the whole being born on a pedicel. In the more widely distributed *Althenia*, the anther is single and with one lobe, in other respects the male flower is similar to that of *Lepilaena*.

Graebner divides *Zannichellia* into *Euzannichellia* Graebn. with leaves with "free basal stipules" to which belongs the cosmopolitan *Z. palustris* L.; and *Pseudo-Althenia* Graebn. "with sheathing leaf bases" incorporating *Z. aschersoniana*. There is no mention of leaf arrangement which appears to be alternate, opposite or whorled in *Z. palustris* and persistently alternate in *Z. aschersoniana*.

Apart from the generic description of *Zannichellia* where Graebner writes: ". . . no long peduncle in the male flower, the anthers occasionally paired (interdum binis) with two thecae on a longitudinal excurrent connective.", there is no specific description of the male flower for either species. The illustration of *Z. palustris* shows a shortly stalked apparently bilobed anther, but it is not clear whether by "interdum binis" Graebner meant two such stalked anthers or the four lobed compound anther (which is eight celled when young) of *Z. aschersoniana*. Presumably "two thecae" means two anther lobes which would be four celled when young. The only living material examined of *Z. palustris*, which came from near Rietmonds Poort North East of Calvinia, had male flowers each with two anther lobes.

Subsequent accounts of the male flower in descriptions of *Zannichellia* and *Z. palustris* in general reference works are insufficient and confusing. Jepson (1923-25) writes of *Zannichellia*: "staminate flowers consisting of an anther on a pedicel-like filament,"; Phillips (1926) of *Zannichellia*: "Stamens 1;

filament slender; anther 2—4 thecous.”; Hegi (1935) of *Z. palustris* “Männliche Blüten . . . aus einzigen, seltener (bei kräftigen Exemplaren) aus zwei sitzenden Antheren (die sich dann den Rücken zuwenden) bestehend. Antheren mit 2 länglichen Hälften . . .”; Abrams (1940) of *Zannichellia*: “. . . 2 celled anther on a short pedicel-like filament”; Britton & Brown (1943) of *Zannichellia*: “. . . single 2 celled anther”; Fernald (1950) of *Zannichellia* “staminate (flowers) consisting of a single stamen with a slender filament bearing a 2—4 locular anther;” Adamson (1950) of *Zannichellia*: “Male flowers with 1 stamen, anther 2-lobed”; and Cabrera (1953) of *Zannichellia*: “Flor masculina pedunculada, desnuda con 1—2 anteros 2-tecas.”

It is interesting to note that G. Bentham (1865) wrote of *Z. palustris* “Male flower of one stamen . . . anthers 2 or 4 celled.”

If the male flower of *Z. palustris* persistently consists of one bilobed anther or two bilobed anthers on separate filaments, as opposed to the apparently constant four lobed anther in *Z. aschersoniana*, this could be a distinction of considerable taxonomic importance. The genus *Lepilaena*, with a similar compound condition in the male flower, is separated from *Althenia* on these grounds.

With reference to the female flower, while Graebner never stated categorically that in *Z. palustris* it consisted of more than one carpel, this was implied by the generic description of the female flower, and the inclusion of number of carpels in his key to the species. Section *Euzannichellia* has “fruits frequently two or more”, while section *Pseudo-Althenia* has “fruits single or paired.”

In the generic description Graebner writes: “Female flower with cupular perianth surrounding the base of the carpels. Carpels 1—8”. This condition in *Z. palustris* is illustrated in fig. 34c of their monograph. As has been seen, in *Z. aschersoniana* each female flower persistently consists of one carpel enclosed in its own perianth.

A number of subsequent authors, for example Fernald (1950) and Clapham, Tutin and Warburg (1952) in their accounts of *Zannichellia* consider each carpel as a separate naked female flower, all being enclosed in a common cup-shaped involucre. Again descriptions of the female flower(s) in general accounts of the genus are insufficient, most authors giving carpel number (per leaf axil) as two or more.

It is evident that a revision of description and interpretation of floral morphology in *Z. palustris*, incorporating all the forms of this widespread species, is necessary. This may well lead to the placing of the two species of *Zannichellia* in two separate monospecific genera.

REFERENCES

- ABRAMS, L., 1940. *Illustrated Flora of the Pacific States*. 1: 91.
ADAMSON, R. S., 1950. *Flora of the Cape Peninsula*. p. 35.
ASCHERSON, P. and GRAEBNER, P., 1907. *Potamogetonaceae*. In Engler, *Das Pflanz enreich* 4:2.
BENTHAM, G., 1865. *Handbook of British Flora*. 2:785.
BRITTON, N. L. and BROWN, A., 1943. *Flora of Northern United States and Canada*. 1:89.
CABRERA, A. L., 1953. *Manual de la Flora de los Alrededores de Buenos Aires*, p. 42.
CLAPHAM, A. R., TUTIN, T. B. and WARBURG, E. F., 1952. *Flora of British Isles.*, p. 1211.
FERNALD, M. L., 1950. *Grays Manual of Botany*. 2: 80.
HEGL, G., 1935. *Illustrierte Flora von Mittel Europa*. 1: 205.
JEPSON, W. L., 1923-25. *Manual of Flowering Plants of California.*, p. 66.
PHILLIPS, E. P., 1926. *The Genera of South African Plants*. p. 43.